PHYLOGEOGRAPHY, FOSSILS, AND NORTHERN HEMISPHERE BIOGEOGRAPHY: THE ROLE OF PHYSIOLOGICAL UNIFORMITARIANISM[1]

Bruce H. Tiffney[2]

ABSTRACT

Biogeography is one of the most synthetic of biological undertakings; it requires placing a substantiated phylogenetic model in a geological, climatological, and ecological context, all of which shift through time. In the past two decades, the application of cladistic and molecular techniques has diversified our grasp on phylogeny. This has allowed the formulation of hypotheses of past distribution patterns based on samples from available living material and algorithms for their interpretation. Fossils contribute to these cladistic approaches by adding morphological checkpoints to character associations in time and by providing a basis for estimates of rates of divergence. However, fossils also check these hypotheses by direct occurrence (does a fossil of the taxon occur where predicted?) and by ecological suitability (is it reasonable that the taxon could occur in the predicted environment?). The first test is straightforward if difficult, requiring the finding of a specific fossil in a specific place and time. The second is based on the assumption of physiological uniformitarianism—that fossil and modern taxa united by a common morphology possess similar physiologies. If correct, then hypotheses of past distribution must accord with the predicted physiological tolerances of the taxon in question. Application of physiological uniformitarianism to phylogeographic hypotheses, together with new paleontological data, suggest (a) the validity of many established phylogeographic hypotheses; (b) the need to reevaluate others; and (c) the recognition that the North Atlantic land bridge likely functioned as a link between the Old and New Worlds into the Later Tertiary, contrary to this author's earlier papers.

Key words: Bering land bridge, boreal, fossil plants, North Atlantic land bridge, Northern Hemisphere, phylogeography, phytogeography, Tertiary, uniformitarianism.

The classic approach to the use of fossils in establishing historical biogeographic hypotheses was essentially scientific but not especially satisfactory. One would survey the known fossil record, assemble the reputable records of the taxon in question, and then suggest a pattern of migration consistent with their distribution in space and time. The resulting hypothesis was constrained by known deposits and existing identifications. This hypothesis could be predictive (it might suggest where new specimens could be expected to be found in time and space), but often the necessary fossil deposits to test the prediction were lacking. Furthermore, the discovery of a new representative of a given clade in an unpredicted time or place often required the hypothesis to be completely reconceptualized. Thus, advances took new data into account, but not infrequently left a historical trail of contradictory hypotheses. It would be far more satisfactory to narrow the possibilities through iterative testing and the refutation of a priori predictions (cf. Platt, 1964).

Recent advances in molecular techniques and data analysis provide a complementary approach to paleontology that helps to constrain phytogeographic hypotheses to a greater degree. Using molecular analyses of genetic material from living plants, coupled with analysis of morphological characters, practitioners invented the field of phylogeography (coined by Avise et al., 1987), overlaying phylogenetic interpretations on fossil and modern biogeographic patterns (e.g., Wen, 1999, 2001; Xiang et al., 2000; Donoghue et al., 2001; etc.). Furthermore, based on the gross assumptions of the molecular clock, phylogeographic hypotheses can also predict the time of phylogenetic splitting, placing a particular clade in a particular geographic locale at a particular geologic time, which creates a testable hypotheses based largely on non-fossil data. This is an important advance, as Donoghue et al. (2001: S41) note: "Geological and climatological processes that have impacted the biota of the Northern Hemisphere during the Tertiary are expected to yield little resolution when area cladograms are compared without taking the timing of diversification into account." Thus, phylogeographic approaches have the potential to offer alternative hypotheses to those generated from

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[2] Department of Earth Science and College of Creative Studies, University of California–Santa Barbara, Santa Barbara, California 93106, U.S.A. Bruce.Tiffney@ccs.ucsb.edu or Tiffney@geol.ucsb.edu.

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paleontological data alone. However, fossils retain an important role in this brave new world. First, the calibration of the clock for a particular clade is dependent on its antiquity as defined by the fossil record. This is a process that involves many assumptions and is fraught with complications that have been the focus of several presentations in this issue (Burnham, 2008; Gandolfo et al., 2008; Nixon, 2008). Additionally, Shaw and Small's (2005) caution on using molecular data from a single specimen, rather than exploring the potential for molecular variation within a species through multiple samples, deserves wider recognition. Second, fossils offer both a direct and an indirect method for testing phylogeographic hypotheses. Considerations of these tests and, particularly, the ecological fit of past distributions into phylogeographic models form the core of this paper.

Modes of Testing Phylogeographic Hypotheses with Fossils

DIRECT TESTING—THE RIGHT FOSSIL IN THE RIGHT PLACE

A phylogeographic hypothesis may suggest the presence of a particular clade at a particular geologic time in a particular geographic place. In general, the most important of these predictions will involve migrational bottlenecks. Thus, in the present case, the focus is on intercontinental disjunctions of taxa between the New and Old World in the Northern Hemisphere, in which the two greatest barriers are the Pacific and Atlantic oceans. These, in turn, create two bottlenecks over which terrestrial organisms need to pass—the Bering land bridge (BLB) and the North Atlantic land bridge (NALB). The former is still in existence, although limited by seasonal climate, while the latter has been affected both by oceanic widening (plate tectonics) and global cooling (Tiffney & Manchester, 2001).

The estimated time of the onset of genetic divergence logically should correspond to the origin of the interruption of gene flow. This interruption could result either from a migration event across a barrier causing the establishment of a new, isolated population or from the vicariance of a pre-existing and perhaps long-established distribution. These alternatives cannot be distinguished from molecular data, although a pre-existing fossil record can support the latter. However, both hypotheses imply the presence of representatives of one or both clades involved in the disjunction at the geographic locality that is inferred to form the barrier-to-gene flow at the time of its interruption.

If a phylogeographic hypothesis thus predicts the presence of a taxon in a particular place at a particular time, then paleontological data may be sought in the appropriately located and aged rock. For example, Donoghue et al. (2001) predicted that *Weigela* Thunb. and *Diervilla* Mill. (Caprifoliaceae) split ca. 5.2 ± 0.5 million years ago (Ma) to establish a present-day eastern Asian (*Weigela*)–eastern North America (*Diervilla*) distribution. The clade was hypothesized to have arisen in China or Japan and to have migrated over the BLB to North America.

At the time Donoghue et al. (2001) wrote, they were not aware of any fossils of *Weigela* or *Diervilla* in the Bering region. However, White et al. (1999), in a fairly obscure publication, place pollen similar to that of *Weigela* and *Diervilla* in northwestern Canada and Alaska, appearing 15 Ma and disappearing ca. 6.5 Ma. While the fossils suggest an older first appearance in the area and a slightly older disappearance than that suggested by phylogeography, the agreement is quite acceptable and the hypothesis is not refuted. However, it is to be noted that *Weigela* also occurs in the European Miocene and Pliocene (Mai & Walther, 1988; Mai, 2001) and that the hypothesis of a North American–European link must still be at least acknowledged.

INDIRECT TESTING—PHYLOGENETIC UNIFORMITARIANISM

Phylogeographic hypotheses place specific taxa in specific places at specific times. When they do so, the general ecological context of the surrounding vegetation should be in accord with the physiological tolerances of the living members of the clade in question. To use a trivial example, the Palmae are classically subtropical and tropical in distribution; a phylogeographic hypothesis that placed a palm in a temperate or boreal context would violate our understanding of the physiologic tolerances from modern examples.

This interpretation is based on the assumption of physiological uniformitarianism. Succinctly, we identify taxa in the fossil record by their morphology, assigning them to living families, genera, or occasionally species in the assumption that similar morphologies reflect similar underlying genotypes. However, the taxa in question also possess unique physiological characters that are again genetically controlled. If we make the identification of *Vitis* L. in the fossil record, we assign it to the genus on the basis of morphology and assume that it represents a liane, as *Vitis* is overwhelmingly dominated by vines (Mabberley, 1997). Similarly, we assume that it brings with it a set of physiological tolerances that allows it to grow in specific thermal and moisture regimes that fall within the tolerances of modern species within the genus. In the case of *Vitis*, this results in a very broad range of ecological tolerance, as the genus extends from temperate to subtropical areas in the Northern Hemisphere (Tiffney & Barghoorn, 1976; Mabberley, 1997).

An alternative possibility must be considered: that morphology has remained sufficiently stable over time to allow placement of a fossil in a modern taxon while physiology has evolved independently, dissociating ecological tolerances from morphological identifications. If this were the case, flora and vegetation would exhibit a similar dissociation through time, and no clear relationship would be observed between cohorts of taxa and specific climates. While the nature of biological systems is too variable to state that this has never happened (e.g., that a genus of subtropical angiosperms evolved a temperate species to cross through a cooler climate, which, in turn, gave rise to a subtropical species upon re-encountering warm climates), the coherence of the history of vegetational and floral change through the Tertiary (e.g., Tiffney, 1985; Mai, 1995; Graham, 1999; Tiffney & Manchester, 2001), in concert with climatic change adduced from other sources (e.g., isotopic sources, Zachos et al., 2001), suggests that physiology is generally stable and tracks morphology.

To date, my discussion has implied that the physiological tolerances are those involving moisture and seasonal warmth. However, there are other aspects of physiology that potentially play an important role in determining clade survival in a given environment. Chief among these is the annual distribution of light at the poles. In previous papers (Tiffney, 1985, 1994, 2000), I have queried whether extended periods of polar winter darkness might prove to be a barrier in the Northern Hemisphere to the migration of evergreen taxa in periods of global warmth, as respiration would carry on in the absence of photosynthesis. If so, evergreen lineages might be restricted to more southerly migration routes in order to balance respiration with a minimum level of photosynthesis. This assumption appeared reasonable, given (a) the frequency of deciduous taxa in the fossil record of the North Pole (Falcon-Lang et al., 2004; Brentnall et al., 2005), (b) earlier experiments (Read & Francis, 1992), and (c) the importance of some deciduous taxa (e.g., *Larix* Mill.) in boreal realms in the present day. While this is a rational conclusion, in fact the current global climate is sufficiently cold that we do not have the opportunity to observe the response of thermophilic evergreen taxa to extended periods of darkness, as could have potentially occurred at times in the Paleogene of the Northern Hemisphere. Recent experiments suggest that the carbon loss involved in seasonal leaf shedding is far greater than the loss involved in dark-season respiration (Royer et al., 2003; Osborne et al., 2004) and that some feature other than carbon balance must drive the prevalence of deciduous taxa in the boreal realm. Brentnall et al. (2005) suggested that this feature reflected the frequency of fire-based disturbance. Such experiments are conducted over brief time spans; in order to survive and migrate, evergreen plants would have to succeed over a multigenerational time frame, allowing reproduction, dispersal, seedling germination, and establishment through repeated cycles. Further examination of both the role of carbon balance and/or fire seems in order, especially since another pattern of note is that many extant high-latitude austral taxa are evergreen. Other features may be involved in explaining the apparent barrier to evergreen taxa; these might be ecological (e.g., Givnish, 2002) or involve phylogenetic constraints inherent in the boreal taxa involved.

If we accept the reality of physiological uniformitarianism, then its application to testing phylogeographic hypotheses has one very useful aspect; it does not require the occurrence of the taxon under investigation in a particular place in the fossil record. As long as there is a fossil flora or fauna with sufficient detail to allow estimation of the paleoenvironment, or even a good geochemical estimate of paleotemperature, one can infer whether the particular taxon in question would logically have survived in the predicted environment.

However, this advantage is balanced by disadvantages. Foremost, it can only be applied to living taxa wherein the physiological tolerances of light, moisture, temperature, etc., are fully known. Furthermore, it cannot be effectively used on taxa with very broad tolerances. It would be difficult to support or falsify a historical hypothesis about a subtropical taxon if it were predicted that its occurrence fell within the scope of a warm-temperate vegetation. This aspect becomes more problematic in the earlier Tertiary where reduced climatic gradients allow the widespread occurrence of equable climes with interdigitated temperate and subtropical taxa. Nevertheless, the method still has power to refute hypotheses where the environmental tolerances of the taxon in question are substantially different from those of the predicted environment of occurrence.

SOME TESTS EMPLOYING PHYSIOLOGICAL UNIFORMITARIANISM

From the foregoing, we can proceed to look at a number of taxa for which phylogeographic hypotheses have been made, placing them in particular geographic situations and climates.

THE BERING BRIDGE

The BLB is a frequently invoked route of exchange between the Old and New Worlds in the Tertiary (Tiffney, 1985; Tiffney & Manchester, 2001). Several southern Alaskan Eocene floras hosted evergreen thermophilic lineages (Wolfe, 1972, 1977), which may indicate that the bridge was open to evergreen lineages at this time (see discussion in Tiffney & Manchester, 2001: S7). Later Eocene through Oligocene floras displayed an increasing dominance of warm-temperate to temperate deciduous taxa (Wolfe, 1972, 1992). By the Early to Middle Miocene, Alaskan floras hosted moderate- to cool-temperate taxa (e.g., Juglandaceae, Fagaceae, *Liquidambar* L., *Nyssa* L., *Tilia* L.; Leopold & Liu, 1994; White et al., 1997, 1999).

Many of the older crossings hypothesized from molecular evidence fit well within the physiological tolerances of the taxa involved. *Rhus* L. was suggested to be present on the BLB at ca. 34 Ma (Yi et al., 2004), *Menispermum* L. at ca. 29 Ma (Lee et al., 1996), *Campsis* Lour. at ca. 24.5 Ma (Wen & Jansen, 1995), *Gleditsia* L. and *Gymnocladus* Lam. at ca. 15–20 Ma (Schnabel et al., 2003), and *Liquidambar* L. at or before 15.6 Ma (Ickert-Bond & Wen, 2006). These are all warm-adapted, mesic taxa, and all but *Rhus* are deciduous; the latter includes deciduous and evergreen taxa.

Several more recent (Late Miocene–Pliocene) hypothesized crossings also fit within the predictions of physiological uniformitarianism. Thus, Nie et al. (2005) predict that *Kelloggia* Torr. ex Benth. (Rubiaceae) crossed the Bering Bridge ca. 5.5 Ma. Its distribution in montane western North America (viz. Burke Herbarium, 2006) and cool Asia fits this hypothesis. Nie et al. (2006a) predict that *Symplocarpus* Salisb. ex Nutt. and *Lysichiton* Schott (Araceae) crossed the Bering Bridge ca. 4–7 Ma. This, again, appears consonant with the Late Miocene–Pliocene Beringian vegetation and ecology of the extant taxa.

However, other hypotheses appear to pose problems for physiological uniformitarianism. Some are marginally problematic. Nie et al. (2006b: 1349) suggest that *Phryma* L. attained its eastern Asia–eastern North America distribution "at least 3.68 ± 2.25 to 5.23 ± 1.37 mya," or in the very latest Miocene through the Pleistocene. *Phryma* has a wide geographic range in North America, ranging from Manitoba to Florida, growing in rich and often moist woods (e.g., Fernald, 1970). Its geographic distribution in eastern Asia (Nie et al., 2006b: fig. 4) suggests an equally temperate environment in southeastern Asia north through Japan and Korea. None suggest an affinity for boreal forest conditions, which would have been present on the BLB and environs during the predicted time of crossing (Leopold & Liu, 1994; White et al., 1999). Nevertheless, *Phryma*'s wide modern distribution, especially in North America, offers the argument that it might be able to slip through the BLB during a brief warm spell within this time frame.

Other taxa are more clearly warm temperate in nature and are harder to imagine making the crossing in latest Miocene and Pliocene. For example, Xiang et al. (1998) proposed that *Calycanthus* L. (now occurring in China, western North America, and southeastern North America—a classic Tertiary refugial distribution, e.g., Li, 1952) crossed Beringia at ca. 3.1 Ma. Wen et al. (1996) and Zhou et al. (2006) place the crossing a little earlier at ca. 6 Ma. Similarly, Wen (1999, after Qiu et al., 1995) suggested that *Magnolia tripetala* (L.) L. split from *M. officinalis* var. *biloba* (Rehder & E . H. Wilson) Y. W. Law of China ca. 2–5.5 Ma. By 6 Ma, marginal exotics that had been present even two million years earlier (Reinink-Smith & Leopold, 2003, 2005) were largely absent from the coastal coniferous forests of Beringia (Wolfe, 1994). Post–6 Ma pollen records from central Alaska suggest a boreal forest (Leopold & Liu, 1994; White et al., 1999) with a few cool-temperate taxa (e.g., *Tilia*, *Corylus* L., *Juglans* L.). In light of its current locales of growth, *Calycanthus* would not be ecologically suited to these environments. While *M. tripetala* does co-occur with *Tilia*, *Corylus*, and *Juglans* in its present eastern North American distribution (Little, 2006), it has a more southern distribution than these other taxa. Additionally, the proposed crossing for *Magnolia* L. overlaps with the opening of the Bering Strait (Gladenkov et al., 2002). The lack of physiological consonance suggests that these phylogeographic hypotheses require reexamination. For example, while Schnabel and Wendel (1998) placed *Gleditsia* in Beringia at 3.9–4.7 Ma, again associated with an implausibly cool flora, Schnabel et al. (2003) re-evaluated this conclusion and placed this crossing in a much more appropriate climatic setting at 15–20 Ma.

While I focus on the bottleneck created by the BLB, in fact, the hypothesis of such a crossing involves more than just the transition across the BLB—it also invokes migration to the bridge and from it to the modern areas of distribution. Thus, a hypothesis involving the crossing of the BLB by *Magnolia tripetala* or *Calycanthus* also must account for the movement from the point of crossing to their present areas of survival in eastern North America, if the postulated time of molecular divergence measures a migrational event. To make this transition, these taxa need not only deal with the ecological setting of the vegetation of Beringia at circa 6 Ma, they must also cross the Rocky Mountains and the interior grasslands before becoming established in the mixed deciduous forests of eastern North America. Given the changing nature of North American vegetation through the Tertiary (Graham, 1999) and the ecological affinities of *Magnolia* and *Calycanthus*, this would be more easily accomplished in the Eocene through Middle Miocene rather than later in the Tertiary.

An alternative hypothesis is that these taxa achieved their distribution at an earlier time, but that the molecular divergence measures the time of their vicariance. This eliminates the objection of the need to migrate through other potentially inhospitable environments, but still leaves the incongruity of *Magnolia* or *Calycanthus* co-associated with boreal taxa in Beringia at the proposed time of interruption of gene flow. This leads me to wonder if, in cases of vicariance or migration, the actual molecular divergence lags behind the time of cessation of gene flow.

THE NORTH ATLANTIC LAND BRIDGE

In Alaska and northeastern Siberia, there is a relatively good fossil record through the Tertiary (Baranova et al., 1989; Wolfe, 1994; Fradkina et al., 2005). Therefore, it is possible to both track ongoing exchange throughout the Tertiary and test phylogeographic hypotheses in this area against fairly numerous taxonomic and ecological data. This has allowed me to be rather black and white in approaching the role of fossils in evaluating molecularly derived phylogeographic hypotheses and focus on support or refutation. Hypotheses and tests lie at the core of science at its best, but often the scientific process is far more labile, resulting not in tests and refutations, but in an awkward upward spiral of understanding as new data modify our interpretation of preceding data. I turn now to just such a case involving the NALB, where I believe that molecular phylogeographic interpretations coupled with new paleobotanical data suggest a changing interpretation of the history of this important exchange corridor.

In earlier papers (Tiffney, 1985, 1994, 2000), I interpreted that the NALB was an important route for biogeographic exchange in the earlier Paleogene based on a range of fossil evidence. Its importance in the late Paleogene into the Miocene was difficult to assess by direct evidence, but plausible arguments for the migration of taxa have been made in the Oligocene (Hably et al., 2000) and Miocene (*Liquidambar*, Ickert-Bond & Wen, 2006). However, post Early Miocene, I was dubious of its significance in light of missing biological (fossil record) and geological data, both to the east and west of Greenland. Our paleontological and geological knowledge of the possible later Cenozoic links between western Greenland and eastern North America remains quite limited but is illuminated by more recent findings.

The fascinating Pliocene flora from Kap København in northernmost Greenland (Funder et al., 1985; Bennike, 1990; Bennike & Böcher, 1990) suggests a tundra vegetation bordering on taiga. To the south and west, Pliocene floras (Vincent, 1990; Matthews & Ovenden, 1990) and insect faunas (Elias et al., 2006) on Prince Patrick, Meighan, Ellesmere, and Banks islands of Arctic Canada suggest a mixed hardwood/conifer forest in the late Tertiary giving way to larch-dominated taiga and tundra by 2 Ma (Vincent, 1990) in some places, and pine-dominated taiga in others (Matthews & Ovenden, 1990), including *Sciadopitys* Siebold & Zucc. on Meighan Island. Precise interpretation of the timing of vegetational change is complicated by a stratigraphy that is still being resolved (Fyles, 1990). Climatic interpretations of entomological fossils (Elias & Matthews, 2002) suggest that the latest Miocene through Pliocene had a lower latitudinal temperature gradient than at present, allowing for the wider spread of the taiga in this period (Matthews et al., 2003).

It would be valuable to trace these transitions back to the Miocene, but only the rich flora from the Middle Miocene Mary Sachs Gravel on Banks Island exists to provide a norm for mid-Tertiary floras of Arctic eastern North America. Interestingly, this flora includes *Glyptostrobus* Endl., *Metasequoia* Hu & W. C. Cheng, *Juglans*, *Liriodendron* L., *Phyllanthus* L., and *Actinidia* Lindl., among other taxa (Matthews & Ovenden, 1990). No further Miocene floras are presently reported between the high Arctic and 35°–40°N latitude in eastern North America. The best continuous evidence for sub-boreal vegetational and climatic change throughout this time frame in the North Atlantic region comes from ca. 50°N latitude in Germany (Utescher et al., 2000).

Turning to geography, we presently lack evidence establishing or refuting possible physical links between western Greenland and eastern Canada south of the northern tip of Greenland in the mid-Tertiary. A second line of evidence for estimating the timing of the opening of the Banks Strait might involve tracking changing biogeographic affinities of marine invertebrates in these waters in response to the opening of the Bering Strait (e.g., Marincovich, 2000), although I am unaware that such data currently exist.

Since publication of my previous papers, several phylogeographic hypotheses have appeared that support later Tertiary exchange via the NALB. For example, Whitcher and Wen (2001: 296) suggested *Corylus* sect. *Corylus* migrated from Europe to North

America "in the late Pliocene or Pleistocene." Realizing both the purported physical barrier and real climatic barrier (taiga and tundra), they invoked long-distance dispersal, perhaps via a bird. This hypothesis requires a lot of the bird, given the distance, the prevailing westerlies, and the size of a *Corylus* fruit. Similarly, Milne (2004), using molecular data, suggested that *Rhododendron* L. subgen. *Hymenanthes* (Blume) K. Koch subsect. *Pontica* Tagg achieved a distribution between Europe and North America ca. 6 Ma or less. Given existing geological and paleontological data, I was predisposed to assume that both timings were anomalously young.

Quite recently, Denk et al. (2005) and Grímsson and Denk (2007) provided an updated evaluation of the Miocene floras of western Iceland, together with a discussion of their geologic setting. These authors placed *Corylus* on proto-Iceland between 12 and 8 Ma in an ecologically suitable temperate flora (vs. the suggested 3–2 Ma via molecular hypothesis) and in the same paper placed *Rhododendron* aff. *ponticum* L. in a 12–10 Ma Icelandic flora (vs. 6 Ma as suggested by Milne [2004]). Their geological analysis focused on the links between Greenland, Iceland, and Europe, and made clear that terrestrial bridges or island stepping-stone options were present through the period, diminishing toward 6 Ma. While their work does not address the Greenland–North America barrier, it clearly indicates the feasibility of a late Tertiary Europe–Greenland link.

In light of these data, the history of both *Corylus* and *Rhododendron* aff. *ponticum* would be consonant with their having achieved a European–North American distribution in the Middle to Late Miocene, followed by a vicariance event. But, as with the Bering example, the molecular data predict that the vicariance event occurred substantially later. Is there any evidence suggesting the possibility of a suitable environmental corridor in the Late Miocene through Pliocene?

Glaciers capable of generating extensive ice-rafted dropstones in the Norwegian–Greenland Sea existed in the Late Eocene (Eldrett et al., 2007), indicating an early development of a cooling climate on Greenland. Ice-rafted debris became more frequent in the mid-Miocene and gathered in strength through the Pliocene into the Pleistocene, but there is evidence to suggest that there was a significant variation in the strength of this process (Thiede et al., 1998). Thus, the ca. 2 Ma taiga-tundra vegetation at the northern point of Greenland (Bennike, 1990) suggests the possibility of a deciduous forest over more southern portions of Greenland in the latest Neogene. It is perhaps worth noting that a roughly 300,000-year warm period in the mid-Pliocene is associated with the re-invasion of Antarctica by *Nothofagus* Blume forests (Hill & Scriven, 1995; Haywood & Williams, 2005), suggesting the feasibility of rapid vegetational response to relatively short-term climatic fluctuations. Repenning (1990) provides an interesting discussion of the interplay of topography, climate, and vegetation in the Late Pliocene and early Pleistocene, hypothesizing short periods of warmth affecting eastern North America north to the eastern Canadian Arctic. While such events have not been clearly demonstrated in the later Miocene or Pliocene of the Arctic, their brief duration would make them difficult to detect, and they might have had an effect on the ability of deciduous taxa to migrate across Greenland as late as the Pliocene or earliest Pleistocene.

In sum, the fossils and the molecules point toward the need to reassess the possibility of a later Tertiary North Atlantic biogeographic link. The NALB may still have been functional in the later Neogene. However, we need more data, especially in Arctic eastern Canada and Greenland. The exposure of sediments with such evidence could become a positive side to current global warming.

One consistent observation that arises in comparing the paleontological and molecular data as presented here is that the fossils and the phylogeographic predictions converge but do not agree on the dates of several Neogene migrations. The molecular data seem to generally predict younger dates than the fossil occurrences or the application of physiological uniformitarianism would suggest. Are paleontologists simply missing data, particularly for short-term climatic fluctuations that open windows of opportunity for migration in the latest Tertiary? Or do most disjunctions arise from the vicariance of pre-existing distributions, as the fossils often suggest? If the latter mode dominates, the discrepancy in timing observed between the fossils and molecular predictions becomes a pattern worthy of investigation. Practitioners of both disciplines have to confer to see if a source of consistent error can be identified, again as discussed by several participants in this symposium.

DISCUSSION

The theme of this symposium was paleobotany in a time of molecular genomics. This could easily be taken as an invitation for paleontologists to weigh the fossil record against the neontological perspectives and tools of molecular systematics. However, at the risk of oversimplification, the question is not the choice of fossils or molecules as has occasionally been propounded by discussants on both sides. Rather, the reality is fossils and molecules. Our two fields exist in a circumstance of reciprocal illumination. Fossils can test predictions arising from molecular phylogenies, and molecular phylogenies can identify possible times and routes requiring further paleontological investigation. To achieve this, both sides must freely discuss their limitations and insights with practitioners of the other discipline.

But there is a further insight from this symposium, one I feel has not been properly realized. The central question is not fossils in an age of molecular phylogenetics but rather the role of desktop computing in both disciplines. This symposium is a testimony to the growth in power of molecular techniques in roughly the past two decades. But these techniques are informative only because of our ability to analyze the immense amount of data they generate using desktop computing. I suggest that the same set of tools will lie at the core of the successful integration of molecular and fossil data to understand the evolution of the flora (or fauna) of the last ca. 60 Ma. I believe we will truly advance only when all paleontological data are easily available online so that molecular phylogeneticists can check temporal calibrations and the goodness of ecological fit of their hypotheses—and this is but one use of such data. To this end, if paleobotany is to be a full partner in evolutionary biology in the age of information, then all verified paleobotanical data need to be databased in an internationally available, online system. Then we can use this summed data to seek and test patterns in evolution and distribution, and fully realize the interdisciplinary power of phylogeography.

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